ANTHECOLOGICAL RELATIONS BETWEEN REPUTEDLY ANEMOPHILOUS FLOWERS AND SYRPHID FLIES. III. WORLDWIDE SURVEY OF CROP AND INTESTINE CONTENTS OF CERTAIN ANTHOPHILOUS SYRPHID FLIES

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ABSTRACT

A worldwide survey of the pollen present in the digestive tract of about 160 syrphid flies of the genera *Melanostoma* and *Platycheirus* and some related taxa confirms the preference of most representatives of this group of Diptera for pollen of nominally anemophilous plants such as *Plantago*, *Typha*, grasses and Cyperaceae. In many cases they had been feeding on pollen of such plants exclusively. The results of this survey are discussed in connection with (especially some ecological) conditions and with the pollination syndromes of such plants.

INTRODUCTION

Representatives of the genera *Melanostoma* and *Platycheirus* (= "M-P group") are effective pollinators of *Plantago lanceolata* L. (Stelleman & Meeuse, 1976, see pt. 1 of this series), and also exhibit consistent feeding visits to grasses and other anemophiles (Van der Goot & Grabandt, 1970; Leereveld et al., 1976; and personal observations by the present author, Meeuse and Stelleman; to be summarised by Stelleman, in prep.). Grabandt (in an unpublished report) and Holloway (1976, New Zealand) confirmed the ambogamous nature of *Plantago lanceolata*, already pointed out by several older workers, by such gut content studies of flies of the M-P group. Strikingly high percentages of pollen of anemophiles, particularly of *P. lanceolata*, were recorded, the first author also mentioning appreciable quantities of grass pollen.

In a description of *Platycheirus* species occurring in Norway, Nielsen (1971) reported, among others, *Plantago lanceolata* as a source of food of several species. Waitzbauer (1976) also noticed a relation between representatives of the M-P group and anemophilous plants when he recorded insect visits of three species of *Platycheirus* to *Typha angustifolia* in Austria. More recently Mesler (1977) noted the frequent feeding visits of the related *Mesograpta marginatus* to *Plantago lanceolata* in Michigan, U.S.A. His descriptions of the feeding behaviour of this syrphid species resembles that of members of the M-P group studied in the Netherlands and in Germany. The present study was aimed at establishing a world-wide validity of the already signalised anthecological relation between members of the M-P group of hover flies and anemophilous plant taxa in western Europe. To this end the gut contents of M-P syrphids hailing from various parts of the world were analysed palynologically.

MATERIAL AND METHODS

The flies, if not collected by members of our research team, were kindly provided by various institutes and collectors in this country and abroad. The total amount of flies at our disposal was about 160 from 15 different countries. Apart from M-P species from Europe material was received from North America and New Zealand. All specimens from New Zealand were referred to *Melanostoma fasciatum*, a species not known from Europe but resembling our *M. scalare* very closely. Two specimens belonged to *Platycheirus immaculatus*, a rare species in the Netherlands. Of the related genus *Pyrophaena* 10 Norwegian specimens of *P. granditarsa* were studied. The 54 localities are not only widely scattered over the world, but are also situated at different altitudes (from sea level to about 1500 m alt.).

Table 1 shows the number of localities per

Table 1. Countries, number of localities and number of specimens used for analysis of gut contents. (Dutch specimens refer to samples; extensive data in Van der Goot & Grabandt (1970)).

Country	no. of specimens	no. of localities	no. of specimens per locality
Canada	5	3	3, 2×1
Czechoslovakia	4	2	3, 1
England	43	1	43
Finland	9	2	5, 4
France	1	1	1
Italy	6	3	3×1
Netherlands	3	3	3×1
New Zealand	15	2	9, 6
Norway	44	11	11, 9, 2×5, 4, 3, 2×2, 3×1
Roumania	8	4	4, 2, 2×1
Spain	2	2	2×1
Sweden	15	10	4, 3, 2, 7×1
U.S.A.	2	1	2
U.S.S.R.	19	8	7, 6, 6×1
Yugoslavia	1	1	1

country and the number of specimens per locality. It appears from this table that the large majority of the specimens came from England, Scandinavia and Russia, which (owing to the local floral composition) may cause a certain bias when conclusions are drawn from the analyses of the gut contents. The number of specimens from Canada and the USA is unfortunately rather scanty. The preparation was carried out as follows.

Every individual specimen was treated in an almost boiling 10% KOH solution for about 5 min. in order to soften the outer chitin skeleton for further manipulation. If the boiling period is extended the fly may come apart and pollen escapes from the digestive tract, so that excessive boiling must be avoided. Since many specimens had been mounted on needles and the holes in their bodies might cause a leakage of pollen during the boiling, it was deemed recommendable to boil needle-mounted flies needle and all. Still, during excessive boiling some pollen may escape through the perforations in the body alongside the needle. Another complication is the chemical reaction between KOH and the metal of the needle often leading to the formation of ferric hydroxide which may precipitate in the form of flakes, thus obscuring the microscopical observation. Also for this reason the treatment with hot KOH solution must be kept as short as possible. To the KOH solution with the specimen a few drops of a solution of safranin in distilled water are added. The safranin stains the exine, which is indispensable for the subsequent microscopical identification. After the insect has been rinsed under a strong jet of distilled water (so as to rinse away pollen grains adhering to the body), it can be dissected in a simple way on a glass slide under a binocular microscope. By means of fine needles and tweezers the outer skeleton is ruptured in order to expose the digestive tract. When excessive amounts of pollen were present (a swollen abdomen of a fly is indicative!) two slides were prepared, one of the anterior part of the tract (in head and thorax) and one of the posterior part (in the abdomen). In this way at least some indication may be acquired of a possible change in the feeding behaviour in a fairly short timespan. A second advantage is a practical one: a very large quantity of pollen in one slide is not sufficiently surveyable. Finally the pollen preparation is mounted in glycerin jelly and the cover glass is sealed off on all sides by means of paraffin wax.

Since our palynological department has an extensive standard pollen collection of slides prepared by means of the customary acetolysis process of Erdtman, it would have been an obvious choice if the same treatment would have been applied to the pollen extracted from flies, but in view of a desirable minimum of loss of pollen and a preferably least complicated procedure, the above-mentioned simple method of preparation was followed.

The pollen identifications were primarily based on Erdtman et al. (1961). Pollen of Plantaginaceae, irrespective of the country of origin,

was referred to four types: the *P. coronopus*, the *P. lanceolata*, the *P. major* and the *P. maritima* types. In addition the slide collection was consulted and also a small reference collection of pollen of *P. lanceolata*, *P. media*, *P. major*, *P. coronopus*, and *P. maritima* especially made for the purpose and prepared in the same way as the flies by treating the whole anthers of these plants in KOH, etc. This collection, when used for comparison, already indicated that the pollen grain diameters reported in the above-cited Scandinavian pollen flora are of very little use; the variation in size is particularly great in *P. lanceolata*, even in pollen extracted from a single anther. Pollen of grasses and Cyperaceae was not further identified, firstly because this would require an appreciable experience (which was lacking) and secondly because there was no suitable reference collection available. During the identification the pollen of reputedly or possibly anemophilous forms such as species of *Typha* and *Salix* were separately recorded.

The counts were performed as follows: if the number of grains did not exceed 500 they were all identified as far as possible, but if it exceeded 500, a homogeneous portion of the slide was selected at a magnification of about 400× and three separate counts of 100 grains were made of which the mean value was taken.

Results

Some specimens studied did not have any pollen in their digestive tract. This may be attributable to three causes, viz., (1) a catch before anthesis of the food plants had taken place (not very likely), (2) a poor or diseased condition of the fly (not so obvious either), or (3) consumption of nectar only (this was noticed by personal observations of particularly *Platycheirus scutatus*, while nectar consumption of M-P syrphids has been also reported by other workers).

The majority of the specimens studied yielded substantial amounts of pollen, as already mentioned, but the effect of the digestive juices on the grains, especially on the ectexine sculpture, renders well-digested pollen unrecognisable owing to a reduced affinity to the stain, to the corrosion and abrasion of the surface, shrinkage and shrivelling of the grains, etc. The latter damage is partly caused by dehydration and by the mechanical action of compression and peristaltic movements of the gut.

Fortunately there are usually enough better preserved, identifiable grains to get some idea of the diet. An additional complication is that the staining of the contents of the digestive tract starts at the oral end and not or hardly from the anal end, so that the pollen grains consumed latest are usually also the best stained. Occasionally the staining was poor because the throat was blocked during the boiling process. Grass pollen seems to have a lower affinity to the safranin dye than dicotyledonous pollen, and pollen grains of Cyperaceae have hardly any, but, even when not stained, are conspicuous by their own brownish colour. Among the flies there were some caught at the beginning of this century. Without exception the pollen in their digestive tract had undergone a process of aging which gave them the appearance of fresh pollen subjected to the standard Erdtman process of acetolysis. This may be a way to procure naturally aged pollen of certain species.

The results of the analyses are shown in table 2 in which four categories are distinguished, three consisting of pollen of easily identifiable anemophilous forms, and the fourth including the remainder. If it was deemed to be relevant (and possible!) to provide some additional information concerning other anemophiles, the *Plantago* types other than the *P. lanceolata* type, and the relative amounts of pollen types present; these are separately entered in the fourth column. Although the specimens were always rinsed to wash away any pollen attached to the outer surface of the body, some may have got into the slide, but at the worst the number, as far as can be ascertained, does not exceed 5 grains per fly and is, therefore, negligible. When only very few identifiable pollen grains were present in the slides the absolute number (and no percentage) is given, while the "+" symbol means that the category is represented only sporadically.

From previous studies of our research group (see parts I and II of this series) the feeding habits of the pollenconsuming members of the M-P type are dependent on (a) the local habitat and stands of vegetation, (b) the time of the day (consumption mainly taking place before 10.00 hrs or 11.00 hrs) and (c) the weather. Such data were not available for the specimens sent to us, but one may infer that especially the first factor is important because the diet sometimes clearly reflects the only available sources (see under "Discussion").

After excessive feeding in the early morning pollen is usually present in the animal body for several hours after the last consumption has taken place and animals caught later in the day still

Table 2. Results of analyses of gut contents of syrphid flies of the M-P group. Explanation in text. Abbreviations used: tricolp.: tricolporate (dicotyledonous pollen type; verruc(ulate), psil(ate), fenestr(ate), retic(ulate), percolp(ate), scabr(ate): Compos. — Ligul. = Compositae Liguliflorae. Records in parentheses: duplicate slides.

Slide no. and country of origin	pollen composition recorded: grasses	*Plantago lanceolata* type	Cyperaceae	other ones
		Melanostoma mellinum		
♀ PAL 7, Netherl.	100%			
PAL 23, Italy	100%			
(PAL 24, Italy	100%)			
PAL 31, Italy	100%			
PBL 21, Roumania	67%			14% Tiliaceae, 14% Pteridophyta 5% other kinds
PBL 25, Roumania	314			7 other ones, 1 prob. Caryophyllac.
PBL 26, Roumania	100%			*P. major* type (= *P. media*): +
PBL 70, England	100%			tricolp.-reticulate: +
(PBL 71	100%)			
PBL 75, England	100%			
PBL 78, idem	100%			
PBL 84, idem	100%			
PBL 89, idem	100%			
PBL 94, idem	100%			
PBL 99, idem	100%			
PCL 7, idem	100%			
PCL 8, idem	100%			
PBL 79, idem	98%			2% tricolp.-echinate
PBL 81, idem	62%			38% Compos.-Ligul.
PBL 82, idem	94%			6% Compos.-Ligul.
PCL 1, idem	88%			12% dicotyl., 2 types
PCL 6, idem	89%			11% mainly tricolp.-retic.
♂ PAL 14, Netherl.	100%			+
PAL 56, USSR	100%			
PAL 72, Norway	95%			5% fenestrate (prob. Compos.-Ligul.)
PAL 79, Norway	86%			14%, mainly Rosaceae
PAL 82, Norway	94%		6%	
PBL 52, Sweden	62%	38%		
PBL 83, England	100%			
PBL 87, England	100%			
PCL 11, England	100%			
PBL 74, England	96%			4% tricolp.-verrucul.
PBL 95, England	98%			1% tricolp.-echinate, 1% tricolp.-reticul.
♀ PAL 9, Netherl.	4%	96%		
PAL 17, Czechosl.	10%	90%		
PAL 21, Yugosl.		100%		
PAL 25, Spain	18%	80%		2%
(PAL 26, Spain	30%	70%)		
PAL 51, USSR		100%		
(PAL 52, USSR		100%)		+)
PAL 55, USSR		100%		
PAL 75, Norway	28%	48%		24% mainly of one type
PBL 30, USA		95%		5% fenestrate (prob. Compos.-Ligul.)
PBL 31, USA		100%		

Table 2 (cont.)

Slide no. and country of origin	pollen composition recorded: grasses	*Plantago lanceolata* type	Cyperaceae	other ones
		(*Melanostoma mellinum*, cont.)		
♂ PAL 27, Spain		95%		5% of one type (rosaceous)
PAL 81, Norway		67		
♀ PAl 32, Finland			100%	
(PAL 33, Finland			100%)	
PAL 34, Finland			100%	
(PAL 35, Finland			100%)	
PAL 36, Finland			100%	
PAL 53, USSR		30%	70%	
(PAL 54, USSR			100%)	
PAL 73, Norway			100%	
(PAL 74, Norway			100%)	*Pinus* (a single grain)
PBL 53, Sweden			85%	15%, 2 *Picea*, 1 prob. Caryophyllac.
♂ PAL 57, USSR			90%	10% triporate-psilate, one *Pinus* grain
PBL 34, Sweden			100%	triporate-psilate: + other types: +
♀ PAL 16, Czechosl.				98% Rosaceae (*Potentilla anserina* subtype, 2% *P. erecta* subtype), other types: +
PAL 22, Italy	32%			68% dicotyledonous, tricolp.-scabrate
PAL 77, Norway	45%			55%, mainly of one type
(PAL 78, Norway	do.)			(do.)
PBL 22, Roumania	18%			prob. 82% Caryophyllac.
PBL 23, Roumania				88% *P. major* type, 10% dicot. tricolp.-reticulate, 2% other types
PAL 30, Italy				93% *P. major* type, 7% Rosac.
PAL 58, USSR				100% *P. major* type (= *P. media*)
PBL 24, Roumania				104 tricolp.-scabr., 4 *P. major* type (= *P. media*), other types: 3
♂ PAL 1, France				100%
PAL 76, Norway				100% fenestrate type
PAL 80, Norway				mainly Ericaceae and Rosaceae, Caryophyllac.: +
♀ PBL 35, Sweden				contained no pollen
		Melanostoma scalare		
♀ PBL 76, England	100%			
PBL 85, England	100%			Ranunculaceae: +
PBL 88, England	100%			tricolp.-echinate: +
PBL 90, England	100%			
PCL 3, England	100%			+
		(*Melanostoma scalare*, cont.)		
♀ PCL 5, England	100%			
PCL 12, England	100%			triporate-psilate: +
♂ PBL 68, England	100%			dicots: +
PBL 72, England	100%			

Table 2 (cont.)

Slide no. and country of origin	pollen composition recorded			
	grasses	*Plantago lanceolata* type	Cyperaceae	other ones
PBL 86, England	100%			
PBL 92, England	100%			dicots: +
♀ PBL 77, England	93%			44 grains tricolp.-echin., 3 other ones
PBL 91, England	91%	9%		
PBL 98, England	88%			12% mainly Ranunculaceae
PCL 4, England	96%			4% Rosaceae
PCL 10, England	79%			21% tricolp.-reticulate
♂ PBL 67, England	90%			10% tricolp.-echinate
PBL 96, England	94%			6% tricolp.-echinate
♀ PBL 80, England		100%		
PBL 93, England				nearly 100% Rosaceae
PCL 2, England	23%			77% tricolp.-reticulate
♂ PBL 69, England	+			100% Compos.-Ligul., other types: +
♀ PBL 97, England				1 Rosaceae, 1 tricolp.-echinate, 1 indeterminate
♂ PAL 83, Norway				100% Rosaceae
PAL 84, Norway				100% Compos.-Ligul.
PBL 40, Sweden				100% mainly 2 types of dicots
		Melanostoma fasciatum		
♀ PBL 51, New Zeal.		100%		
♂ PBL 43, New Zeal.		100%		
PBL 44, New Zeal.		100%		
PBL 45, New Zeal.	+	100%		+
PBL 46, New Zeal.		77%		33% mainly 4 types of dicots
PBL 47, New Zeal.		65%		35% do.
PBL 48, New Zeal.		100%		
PBL 50, New Zeal.		100%		
PBL 49, New Zeal.	esophagus	5%		80% Malvaceae, 15% Compos.-Ligul.
	gut:	6%		89% Compos.-Ligul., 5% Malvaceae, other types: +
♀ PBL 59, New Zeal.	100%			+
PBL 61, New Zeal.	81%			19%
PBL 64, New Zeal.	91%			9%
♂ PBL 62, New Zeal.	84%	1%		15%
PBL 63, New Zeal.	100%			+
♀ PBL 60, New Zeal.				100%
		Platycheirus clypeatus		
♀ PAL 19, Czechosl.	1			2 not identifiable
(PAL 20, Czechosl.	6	3)		(2 not identifiable, 4 of different types)
PAL 28, Italy	100%			
PAL 29, Italy	100%			
PAL 40, Finland	100%			
PAL 46, Canada	100%			
(PAL 47	100%)			

Table 2 (cont.)

Slide no. and country of origin	pollen composition recorded			
	grasses	*Plantago lanceolata* type	Cyperaceae	other ones
PBL 3, Norway	100%			+ triporate-scabrate
PBL 4, Norway	100%			
PBL 27, Roumania	100%			+
PBL 28, Roumania	100%			
♂ PAL 99, Norway	87%			12% *Rumex*-like, 1% differ.
(PAL 100, Norway	do.)			(do.)
PBL 1, Norway	130			4 *Rumex*-like, 4 different
PBL 5, Norway	2		1	1 tricolpor.-reticul.
PBL 6, Norway	100%			do.
PBL 7, Norway	100%			
PAL 18, Czechosl.		100%		
PBL 8, Norway		100%		
♀ PAL 37, Finland			100%	
(PAL 38, Finland			100%)	
♂ PBL 33, Sweden			100%	
PBL 54, Sweden	11%		86%	3%
♀ PAL 39, Finland				72% Comp. Ligul., 28% *Melampyrum*
PBL 2, Norway	+			100% dicotyl, pericolp.-scabrate, other types: +
♂ PBL 41, Sweden	47%		4%	49%, mainly 2 tricolp. dicot types
PAL 45, Canada				contained no pollen
PBL 38, Sweden				contained no pollen
		Platycheirus angustatus		
♀ PBL 73, England	100%			
PAL 50, Canada			100%	1 *Pinus*
		Platycheirus scutatus		
♂ PAL 85, Norway		1		100% of 2 tricolp. types
PAL 86, Norway				100% of 3 tricolp. types
PBL 32, Sweden				contained no pollen
		Platycheirus albimanus		
♀ PAL 59, USSR				100%, mainly 2 types
PAL 62, USSR		10		13, 3 types
PAL 64, USSR				100% fenestrate
PAL 97, Norway			+	100% tricolp.-scabrate
PAL 98, Norway				ca. 50 fenestrates
PBL 36, Sweden				100% mainly Caryophyllac. and tricolp. types
PBL 37, Sweden				100%
PBL 42, Sweden	+			various types + *Typha latifolia*
♂ PAL 60, USSR				mainly Ericaceae + various tricolp.
PAL 61, USSR				100%
PAL 63, USSR				100% various
PAL 65, USSR		3		24 tricolp.-psil., 15 indeterminate, 1 different
PAL 95, Norway				mainly tricolp., fenestrate, and tricolp.-psilate types
PAL 96, Norway				various types

Table 2 (cont.)

Slide no. and country of origin	pollen composition recorded: grasses	*Plantago lanceolata* type	Cyperaceae	other ones
PBL 39, Sweden				mainly Caryophyllac., also tricolp. types
		Platycheirus fulviventris		
♂ PAL 13, Netherl.	93%	4%		3% prob. Caryophyllac.
		Platycheirus immarginatus		
♂ PAL 87, Norway	93%		7%	
PAL 88, Norway	+		100%	
		Platycheirus peltatus		
♀ PAL 90, Norway			71%	12% Caryophyllac., 17% other types
PAL 66, USSR				100%
PAL 70, USSR		3%		97% various
PAL 71, USSR			37%	66%
PAL 89, Norway				50% *Rumex*-like, rest one type
♂ PAL 67, USSR				100%
PAL 68, USSR				100%
PAL 69, USSR				100%
PAL 91, Norway				100% Liliaceae
PAL 92, Norway				mainly Rosaceae, also *Typha latifolia*
PAL 93, Norway				mainly Rosaceae
PAL 94, Norway				100%
		Platycheirus scambus		
♀ PAL 42, Finland	100%			
(PAL 43, Finland	100%)			
PCL 9, England	100%			
		(*Platycheirus scambus*, cont.)		
♂ PBL 58, Sweden	100%			
♀ PAL 44, Finland	+		78%	22% *Rumex* sp., *Secale* +
PAL 48, Canada			100%	
PAL 49, North Am.			100%	
♂ PBL 56, Sweden			100%	Pteridophyta: 1
PBL 57, Sweden		28%	72%	
♀ PAL 41, Finland	1		17%	83% *Rumex* sp., *Tilia* +, 1 *Pinus*
PBL 55, Sweden	8%		22%	70% Pteridophyta, various +
		Pyrophaena granditarsa		
♀ PBL 12, Norway	100%			
(PBL 13, Norway	100%)			
PBL 14, Norway	90%			10% trilete + Chenop., + different
♂ PBL 16, Norway	100%			+ tricolp.-scabrate
♀ PBL 9, Norway				100%, mainly one type
(PBL 10, Norway				100%)
PBL 11, Norway				100%, various types
PBL 15, Norway				100%, in two types
♂ PBL 17, Norway				100%, in three types
PBL 18, Norway				100%, mainly in 2 types
PBL 19, Norway				100% Rosaceae
PBL 20, Norway				100% in two types

yield quantities of recognisable pollen. That weather conditions were adverse when the flies were caught is hardly likely because as a rule entomologists do not go out on field trips to catch sun-loving insects when the conditions are unfavourable.

The table does not only show confirmations but also deviations from the general consumption pattern of a certain syrphid species. It also gives some indication of the local habitat at a certain date whenever diverse species are available from the same site and date. The reconstruction of the biotope from the feeding habits of a number of sympatrically occurring hover flies may eventually provide us with a useful record of the consumptive behaviour of a certain syrphid species of the M-P group in that biotope and enables the comparison of that specific behaviour with the general tendencies. Such a systematic study has not been carried out as yet but seems highly promising.

DISCUSSION AND CONCLUSIONS

The usefulness of a pollen vector is to a large extent dependent on the faithfulness of this vector. Generally speaking the efficiency, i.e., the chance of an efficient transfer of pollen, increases as the faithfulness is greater. The consumption of pollen of anemophiles or apparent anemophiles by syrphid flies is only benificial to a plant species if a previous visit was to a flower or inflorescence of a specimen of the same species. This is a salient point in the present investigation because the relatively high degree of faithfulness of the syrphid flies of the M-P group, as established by direct observations and resulting in effective pollen transfers (Stelleman & Meeuse, 1976), is assessable by the composition of the consumed quantities of pollen. The presence of practically only one kind of pollen suggests a strongly monolectic feeding behaviour, and even if fair amounts of only two or three kinds of pollen is consumed, i.e., only a few plant taxa are selectively being visited, the efficiency of the flies as pollinators is not greatly reduced. However, since the groups distinguished may contain several species it would be an exaggeration, not to say misleading, if the insect is called faithful to a single taxon because it is faithful to a type of plant and not necessarily to only one species. It is quite clear that many individuals or even species are faithful to a certain type. Observations in the field of the behaviour of a single fly suggest that in many situations the animal visits only *Plantago*, or only the inflorescences of a single grass species (e.g., one of the few or the only one in anthesis at the time of feeding), or only a single genus of the Cyperaceae (such as *Rhynchospora*), or nothing but *Typha*. Knowledge of the conditions obtaining at the locality (time of the year, floral composition at the site, time of the day, availability and relative frequency of the potential sources of pollen food in the habitat, etc.) may permit the conclusion of a high degree of faithfulness, but this is information usually not available when flies collected without extensive field notes are being studied. Bearing this in mind, one nevertheless arrives at a tentative evaluation of the results of the analyses as shown in table 2.

It seems as if the behaviour is inconsistent and the table rather meaningless, but a perusal of table 2 suggests that ambiguous evaluations may be explained by the local habitat. *Melanostoma mellinum* and other species studied in an environment teeming with *Plantago*, grasses, etc. seem to have feeding preferences, but it stands to reason that in certain vegetation types or in a certain season *Plantago* pollen is not available. Unpublished records of visits of M-P syrphids by P. Stelleman in heathland and moorland areas in the Netherlands in the month of August show that the only opulent sources of pollen available, viz., *Molinia coerulea* and sometimes *Rhynchospora*, are visited. In spring *Typha* may be eaten by flies already active at that time and living near the water containing the stands of *Typha* because no other source may be present at that site at that time. Waitzbauer (1976) recorded *Platycheirus clypeatus*, *P. fulviventris*, and *P. perpallidus* as occurring in large numbers on the male inflorescences of *Typha* from the end of May till the middle of June. Presumably other good sources of pollen were not available at the site at the time (or the producers had not come into flower yet).

Taking all this into account one may safely conclude that at least a majority of the taxa of the M-P group of syrphids occurring in Europe, America, and New Zealand exhibits a feeding behaviour similar to that observed in several sites in Europe (especially in Holland) and are faithful to a certain source of food, sometimes *Plantago*, sometimes grasses, sometimes Cyperaceae (or combinations of these). The flies are obviously capable of discriminating between the plants growing in their habitat and of selecting their pollen sources. An earlier study of gut contents of syrphids of the M-P group including *Pyrophaena* by Van der Goot & Grabandt

(1970) had already shown the feeding preferences of these flies. The present study confirms the deviating consumption pattern of certain species, and suggests that *Platycheirus albimanus* and especially *P. scutatus* are exceptional. *P. scutatus* often feeds on nectar alone (personal observations by our Amsterdam research group in Hessia, Germany) and also differs in its behaviour in that it is actively feeding till late afternoon whereas most members of the M-P group are only active from dawn to 10.00 hrs or 11.00 hrs in the morning.

Pollen of grasses and/or *Plantago* was found in specimens from Europe, N. America and N. Zealand. Pollen of Cyperaceae was only present in appreciable quantities in specimens from Scandinavia, the adjoining part of the USSR, and Canada. This is no doubt attributable to the locally great abundance of cyperaceous forms in open arctic and subarctic vegetation types (heathlands, tundra, etc.).

In other parts of the world more or less local stands of Cyperaceae may attract representatives of the M-P group at least when other pollen sources are not abundant. *Carex* and *Rhynchospora* are visited in, e.g., the Netherlands in special habitats (moorland, fens, etc.).

When this paper had been submitted for publication, a large number of syrphids of the M-P group (about 180) became available for dissection. The results confirm the general picture, viz. that all over the world the diet of such flies consists very often of pollen of nominal anemophiles (Cyperaceae, Gramineae, *Plantago lanceolata*, *P. maritima*, *P. media*), even in such remote areas as Madagascar (*Melanostoma annulipes*: 100% Cyperaceae pollen, almost certainly of a *Cyperus* spec. of the *C. papyrus* group).

Since an effective transfer of pollen of *Plantago* by M-P flies has been demonstrated (Stelleman & Meeuse, 1976) the presence of appreciable quantities of *Plantago* pollen in the digestive tract of such syrphids may be taken as clearly indicative of an effective pollination with the flies as the animal vector. SEM photomicrographs (Stelleman, 1978) have shown that grass pollen may also become attached to the body of M-P syrphids and it is tentatively accepted by the present author that the consumption of grass pollen is indicative of a possible effective pollination of some grasses by these flies. The same probably holds for pollen of Cyperaceae, although so far pollen grains of Cyperaceae have not been found adhering to insect bodies, but this is under investigation.

By assuming that the presence of appreciable quantities of ingested pollen in the digestive tract of a species of syrphid is sufficient proof of a possible effective pollen transfer by the species in question, the final possible, tentative conclusion can be drawn that plant forms with a more or less manifest anemophilous pollination syndrome are not infrequently pollinated by such flies. This plant-insect interaction is found in many parts of the world, so that most species of syrphid flies belonging to the M-P group are apparently specialised feeders. Several questions remain unanswered, such as the possible role of "Pollenkitt" in the adhesion of pollen grains to the insect body, and the relative importance of a possible anemophilous pollen transfer in respect of the effective entomophilous pollination. The study of the topic is continued by our research group in various directions.

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